

DEVELOPMENTAL PLASTICITY AND FECUNDITY IN THE ORB-WEAVING SPIDER *NEPHILA CLAVIPES*

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ABSTRACT. To document variation in several developmental parameters and the effect of this variation on female adult size and fecundity, marked individuals were followed in three disjunct populations of the widely distributed spider *Nephila clavipes* (Araneae: Tetragnathidae). The sites chosen had very different physical and biological conditions which were expected to affect the development of the animals. Several developmental parameters were very plastic, such as weight gain and number of juvenile instars, varying both among and within populations. In contrast, two important developmental parameters, growth per molt and pre-molt weight, were constrained within each population but differed between tropical and temperate conditions. Constraining growth per molt established a developmental trajectory, and variation of its slope and of the number of juvenile instars were the primary causes of variation in adult female size and the correlated variation in the fecundity per egg sac.

RESUMEN. Para explorar la variación en parámetros de ontogenia y la consecuencia de esta variación para el tamaño en hembras maduras, un estudio del campo usando individuos marcados fue hecho en tres poblaciones desconectadas de la araña *Nephila clavipes* (Araneae: Tetragnathidae). Los sitios escogidos presentaban condiciones físicas y biológicas muy distintas, los cuales se anticipaban a influir fuertemente en la ontogenia de los animales. Algunos parámetros ontogenéticos se demostraban muy plásticos, mostrando variación tanto dentro, como entre poblaciones, mientras que otros parámetros fueron menos plásticos. Dos parámetros importantes en el crecimiento de las arañas, el crecimiento por muda y el peso antes de mudar, no variaban dentro de cada población, pero mostraban variación entre condiciones tropicales y templadas. Inflexibilidad en el parámetro de crecimiento por muda produce una trayectoria ontogenética. Variación en el pendiente de tal trayectoria y en el número de estadios juveniles son las causas principales de la variación observado en el tamaño de las hembras maduras.

In a variety of arthropods, variation in adult size has been correlated with differences in male competitive ability, voltinism, female fecundity, and other parameters of fitness (e. g., Lawlor 1976; Harrington 1978; Christenson & Goist 1979; Eberhard 1982; Morse & Fritz 1987; Atkinson & Begon 1987). In insects, correlations of variation in size with environmental and biological factors have been utilized to develop models describing the evolution of arthropod life histories (Tauber & Tauber 1978; Masaki 1978; Mousseau & Roff 1989). Changes in size and voltinism are often correlated with latitude and altitude (Masaki 1978; Mousseau & Roff 1989; Dingle, Mousseau & Scott 1990). However, few studies have investigated the proximal cause of variation in adult size: variation in juvenile development (*cf.* Hugué & Louveaux 1986).

In most insects and spiders, growth is determinate and the age and size at maturity are governed by the number of instars, intermolt du-

ration, and growth at each molt. Variation in juvenile development, due either to genetic differences (Newman 1988a; Mousseau & Roff 1989) or to environmentally induced plasticity (Schmalhausen 1949; Stearns 1983; Stearns & Koella 1986; Newman 1988b), will result in variation in adult size and age at maturity. Size and age at first reproduction are correlated with female fitness in many invertebrates and ectothermic vertebrates, changing female fecundity and the probability of death prior to reproduction. First, female fecundity increases with increased body size (Turnbull 1962; Toft 1976; Harrington 1978; Seigel & Fitch 1984; Palmer 1985; Fritz & Morse 1985; Miyashita 1986; McLay & Hayward 1987; Ford & Seigel 1989) and decreases with increased age at maturity. In an iteroparous annual organism, an early maturing female will have more opportunities to reproduce (Toft 1976, Suter 1990). Second, juveniles of many organisms are more at risk from

Table 1.—Characteristics of sites used, including generations per year (facultatively bivoltine in Veracruz), seasonality and annual rainfall, mean and standard deviation of prey capture rates (per 12 diurnal hours per spider, superscripts refer to significantly distinct groups), and relative predation rates on juveniles less than 0.5 cm t + p (Higgins in press). Climate data sources: Panama: Leigh et al. 1982; Mexico: Garcia 1973; Texas: US Meteorological Service. Prey-capture rates from Higgins and Buskirk, in press.

Site	Study period	Voltinism	Seasonality	Rainfall	Prey capture	Predation
Panama	1/1985–7/1986	2	wet/dry	2.5 m	wet: 2 (9.75) ^a dry: 1 (1.12) ^b	high high
Veracruz	7–11/1986, 5/1987	1	warm/cold	4.5 m	2 (2.71) ^a	high
Texas	7–8/1985, 5/1988	1	warm/cold	1.1 m	1 (0.83) ^b	low

predation than adults; therefore, the probability of death prior to reproduction increases with the duration of the juvenile stages (Bervin & Gill 1983; Stearns 1983; Etter 1989; Higgins in press).

The orb-weaving spider *Nephila clavipes* (Linnaeus) (Araneae: Tetragnathidae) is a broadly distributed organism (Levi 1980) with striking variation in adult female size. I anticipated that variation in female size among populations existing under different conditions resulted from variation in one or several juvenile developmental parameters. Laboratory studies involving males of this spider have revealed food-dependent variation in both growth per instar and the number of instars before sexual maturity, contributing to variation in size at sexual maturity (Vollrath 1983). To investigate the developmental causes of variation in female size and the environmental correlates of the developmental variation, I undertook field studies of marked individuals in three disjunct populations of *N. clavipes*: Barro Colorado Island, Panama, coastal Veracruz, Mexico and southeastern Texas, USA. These data were combined with data concerning female fecundity in the two tropical populations to document the fitness consequences of variation in adult female size.

Study Organism.—*Nephila clavipes* is an orb-weaving spider found from the southeastern United States to northern Argentina (Levi 1980). The spiders have one post-hatching non-feeding larval stage (*sensu* Foelix 1982) and molt to the first instar before emerging from the egg sac. In univoltine populations, a quiescent stage occurs in the egg sac. The spiderlings spend one or two instars together on a tangle web then disperse (Kimmel & Grant 1980; Hill & Christenson 1981). This species is highly sexually dimorphic (Levi 1980). Mature males vary from 0.4–0.7 cm leg I tibia + patella length. Females reach sexual

maturity at a range of sizes, 0.8–2.0 cm leg I tibia + patella length (Higgins pers. obs.). The spiders lay their egg sacs away from the orb and do not usually return, but build in a new site one or two days after laying. The phenology varies among populations, in part related to different weather patterns (pers. obs.), but no marked, free-living mature females have been observed to survive more than five months (over 200 individuals in 7 sites). Among the three populations studied, that on Barro Colorado Island, Panama, is bivoltine with peak female abundances in the early rainy season and late-rainy to early dry season (Lubin 1978; Higgins 1988) and that in Houston, Texas, is univoltine with peak female abundance in August–September (Higgins 1988). In Los Tuxtlas, Veracruz, Mexico, the population is facultatively bivoltine: there is normally only one generation per year with peak female abundance in August–September (pers. obs.). Occasionally, juveniles do not enter winter quiescence and these individuals mature and reproduce in May.

Study Sites.—At all sites, I studied spiders found in second growth (Texas, Panama) or primary (Veracruz) forest and along edges of trails and abandoned roads. During the study, all three sites had maximum daily temperatures of about 27 °C (Garcia 1973; Leigh, Rand & Winsor 1982; Higgins 1987). Patterns of rainfall, prey capture, and predation varied among the three populations and between seasons on Barro Colorado Island (Table 1). The prey-capture rate varied with weather, and was significantly higher in Veracruz and the Panama rainy season than in Texas and the Panama dry season (Higgins & Buskirk in press). The frequency of predator attacks was significantly higher for small juveniles (<0.5 cm leg I tibia + patella length) within each population and higher in the tropical populations compared to Texas (Higgins in press).

Lowland Panama has a seasonal tropical climate (Leigh, Rand & Winsor 1982), the dry season normally lasts from January to mid-May. The southern coast of Veracruz, Mexico, has a wet tropical climate (de la Cruz & Dirzo 1987). Although there is no regular dry season, there is an unpredictable period of winter storms that combine winds, low temperatures, and rain, beginning between September and December and lasting two to four months. The spiders were studied in the eastern section of the biological station "Los Tuxtlas" (Universidad Nacional Autonoma de Mexico). Galveston County, Texas has humid summers with little rainfall and relatively cold winters lasting from November to March (average minimum temperature 11 °C). The spiders were studied in scrub forest at the University of Houston Coastal Center (Higgins 1987). The seasonality of the climate in Panama resulted in replication of dry and rainy conditions between the three populations: Panama dry and Texas, Panama rainy and Veracruz.

METHODS

The data were collected through repeated observations of marked individuals. Each spider was measured (leg I tibia + patella length ($t + p$), $\text{cm} \pm 2\%$, measured with Helios needle-nosed calipers) without removing the animal from its web. I individually marked spiders larger than 0.4 cm $t + p$ on their legs (with "Testor's" flat enamel (Testor Corporation, Rockford, IL 61108, USA)) and flagged their web sites. Spiders were re-marked after molting. Individuals of less than 0.4 cm $t + p$ were not marked, but their web sites were flagged. Spider sex and reproductive status were categorized as: immature (indeterminate sex), penultimate instar male, juvenile female, mature male or female. Animals larger than 0.5 cm tibia + patella length were assumed to be juvenile females as males rarely reach that size without showing secondary sexual characteristics. Mature females have heavily sclerotized external genitalia, distinguishing them from immature females. During the study period (Table 1), I visited each individual regularly (nearly daily in Veracruz, Texas, and Panama in 1985; every other day in Panama in 1986) until it could no longer be found.

Growth.—Growth was divided into two distinct but interrelated measures: (a) growth per molt (change in $t + p$) and intermolt interval (days between molts), and (b) weight gain per

unit time. Between molts, the spiders gain weight by expanding the abdomen volume. At the time of the molt, the leg length and carapace size change.

Growth per molt was determined through comparison of pre- and post-molt $t + p$ length. I also measured $t + p$ of discarded exoskeletons found in the webs of recently molted spiders. The pre-molt $t + p$ length was not different from the exuvia $t + p$ length for the same individual ($n = 19$, paired t test = -0.46 , P (2 tailed) = 0.65). Therefore, I included the length of the exuvia $t + p$ in the analysis of growth per molt when pre-molt $t + p$ was unknown. If an individual was observed for more than one molt, only data from the first molt were included in the analysis of growth per molt. I recorded intermolt intervals (days between molts) for individuals that were observed for more than one molt.

Weight gain over 14 day intervals by females greater than 0.4 cm $t + p$ was estimated in the Panama and Veracruz populations. I chose two-week intervals to reduce the variance in the rate of weight gain during the intermolt cycle (Higgins 1988). As these spiders have approximately cylindrical abdomens, I estimated abdomen volume from abdomen length (cm) and width (cm) as: abdomen volume (ce) = $(\text{length}) \pi (\text{width}/2)^2$. (I found that taking these measures with calipers was less likely to cause web-site abandonment than removing the spiders from their webs to be weighed.) In Panama, I determined that the weight of a spider could be estimated as a function of abdomen volume and leg I tibia + patella length: weight (g) = $0.012 + 0.081 ((t + p)^3) + 0.784 (\text{abdomen volume})$; $R^2 = 0.998$ ($n = 86$, $F_{(1,83)} = 17,701.29$, $P < 0.001$).

Reproduction.—To evaluate the effect of female size on fecundity, I collected first egg sacs from marked free-living females in Panama and Veracruz. Females observed molting to sexual maturity were marked, and only those that were followed until oviposition were included, thereby avoiding age affects in reproduction (Suter 1990). Changes in orb-web renewal behavior signal when a female is preparing to lay (Higgins 1990). I removed gravid females from the field, weighed them, and placed them in $30 \times 15 \times 70$ cm cages in an insectary in Panama or a non-airconditioned laboratory in Veracruz, providing live prey if a viscid spiral was built. Most females laid eggs within 5 days of being collected, and were subsequently weighed and released. Three

to five days after being laid, the egg sacs were opened and the eggs removed, weighed and counted. Whereas living eggs are yellow in color, some egg sacs contained a few grey or dried black eggs that I presumed to be infertile or dead. If more than 10 eggs were grey or black, they were counted separately and the yellow eggs were reweighed. In these clutches, I estimated mean egg weight using only the fertile eggs. I calculated relative clutch mass (RCM) as total egg mass divided by post-laying weight of the female (Seigel & Fitch 1984). Post-laying rather than pre-laying weight was used to ease comparison with the data available for other spiders (McLay & Hayward 1986).

Statistical Analysis.—Many of the variables collected are functions of spider size ($t + p$) or weight. After checking the subsets of data from each site to assure that all had significant regressions, preliminary ANCOVA were run to test for significant interaction effects between the covariate (size or weight) and the factor in question (site, generation or season). If significant interaction effects were found, indicating significant difference in the slopes of the lines being compared, a regression of the entire data set was done saving the residuals; and these were analyzed with ANOVA to test for significant effects of the factor in question. If the comparison of regression lines revealed no significant interaction effect (the lines were parallel), the data were further analyzed with ANCOVA, dropping the interaction term, to determine if the functions had significantly different y -intercepts (Sokal & Rohlf 1981). All analyses were done with SYSTAT, which uses a least-squares algorithm for ANOVA and regression analyses (Wilkinson 1987). Lastly, in biologically significant cases where the null hypothesis was not disproven, indicating similarity between groups, an *a posteriori* power test was calculated. This descriptive statistic gives the minimum difference the test could have detected at $P = 0.05$, expressed as a percent of the mean value (N. Fowler, pers. comm.).

RESULTS

Growth.—Growth was measured as three related factors: weight gain in 14 d intervals, leg I tibia + patella growth per molt and intermolt interval. Weight gain was compared between wet-season Panama and Veracruz; the spiders' web-site tenacities were too low during the Panama dry season to allow observations over two week

intervals. The rate of weight gain varied with size ($t + p$) and sexual status (immature or mature female). In juveniles of both sexes, weight gain was a log function of the spider size ($t + p$) at the beginning of the observation period, with no difference between sites (ANCOVA: no interaction effect; site: $F_{(1,10)} = 2.17$, $P = 0.17$; regression: $\ln(\Delta \text{weight}) = -2.34 + 2.26(t + p)$, $R^2 = 0.626$, $F_{(1,11)} = 18.37$, $P = 0.001$). Weight gain by mature females was independent of size ($n = 11$, $R^2 = 0.002$, ns) and a Mann-Whitney U -test showed no difference between Panama and Veracruz ($df = 1$, $U = 0.11$, $P = 0.84$). Mature females gained weight at a mean rate of 1.622 g/14 d (SD = 0.806).

The development of juveniles was compared by examining the pre-molt weights and the change in size ($t + p$) with each molt. Pre-molting abdomen volume (an estimate of weight), pre-molt size ($t + p$), and post-molt size were related. The volume of the abdomen was measured on the day of the last pre-molt orb, 2–4 days before the molt (spiders cease building orbs before molting). Pre-molt abdomen volume was strongly correlated with the pre-molt size ($t + p$) of the spider and did not vary between the two tropical sites (Fig. 1a. ANCOVA: no interaction effect, minimum detectable difference = 28%. site: $F_{(1,17)} = 0.505$, $P = 0.49$; minimum detectable difference = 28%. Regression: $(\text{abdomen volume})^{1/3} = 0.07 + 0.63(t + p)$, $R^2 = 0.89$, $F_{(1,18)} = 146.0$, $P < 0.001$). The post-molt $t + p$ was highly correlated with the abdomen volume of the individual on the day of the last pre-molt orb and the relationship did not vary between the sites (Fig. 1b. ANCOVA: no interaction effect, minimum detectable difference = 1.9%. site: $F_{(1,17)} = 0.41$, $P = 0.53$; minimum detectable difference = 90%. Regression: post-molt $t + p = 0.04 + 1.88(\text{abdomen volume})^{1/3}$, $R^2 = 0.94$, $F_{(1,18)} = 286.2$, $P < 0.001$).

Intermolt interval in days was highly variable within sites and positively correlated with the spider size (Fig. 2). Comparison of Panama dry, Panama wet, Veracruz and Texas showed no significant effect of site or season (ANCOVA: $n = 31$. site: $F_{(2,27)} = 1.20$, $P = 0.32$; season (Panama dry and Texas vs. Panama wet and Veracruz): $F_{(1,28)} = 0.03$, $P = 0.86$).

Growth per molt was compared through the regression of post-molt size ($t + p$) on pre-molt size (Fig. 3). Male and female growth per molt was compared only for the Panama data set,

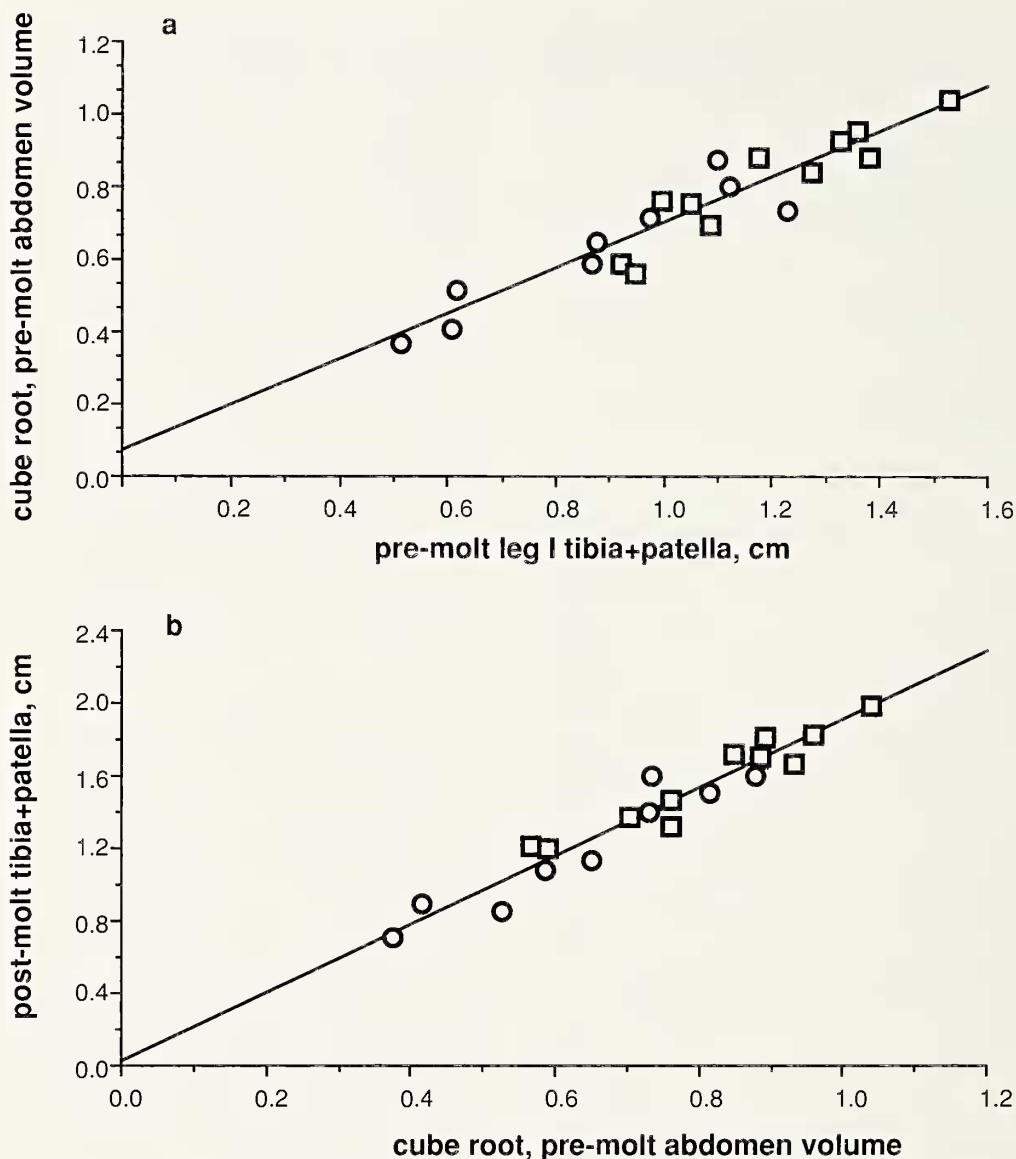


Figure 1.—a. The relationship between pre-molt tibia + patella length ($t + p$) and pre-molt abdomen volume. b. The relationship between pre-molt abdomen volume and post-molt $t + p$. (○ = Panama wet; □ = Veracruz).

which has the largest number of observed male molts. There was no difference between male growth and juvenile and female growth (ANCOVA: no interaction effect, minimum detectable difference = 0.8%. $n = 28$ males, 101 unsexed juveniles and females; sex: $F_{(1, 126)} = 0.6$, ns, minimum detectable difference = 24%). Spiders in the three populations exhibited two different rates of growth per molt. The two generations observed on Panama and the Veracruz

population had the same growth per molt (Table 2) and these data were pooled in the final analysis as "tropical" (between sites minimum detectable slope difference = 0.60%, minimum detectable intercept difference = 16%). In contrast, the population in Texas grew less per molt: the slope of the regression line was significantly lower (ANCOVA interaction term, Table 2). Analysis of the residuals revealed that the early instars were larger in Texas than in the tropics (ANOVA,

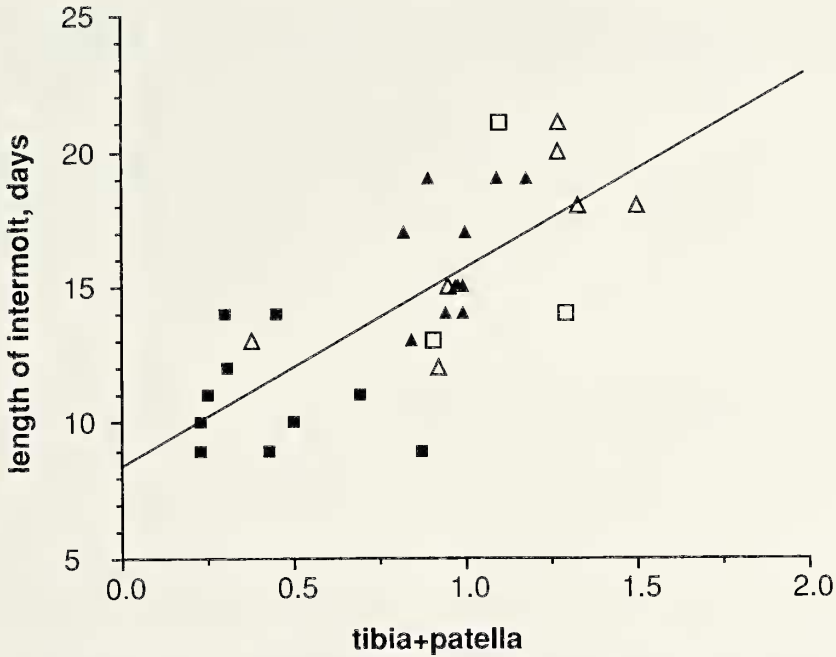


Figure 2.—The intermolt interval in days plotted against tibia + patella length ($t + p$) for all three populations: days = $7.18 + 8.56 (t + p)$, $n = 31$, $R^2 = 0.525$, $P < 0.001$. (Δ = Veracruz; \square = Panama wet; \blacksquare = Panama dry; \blacktriangle = Texas).

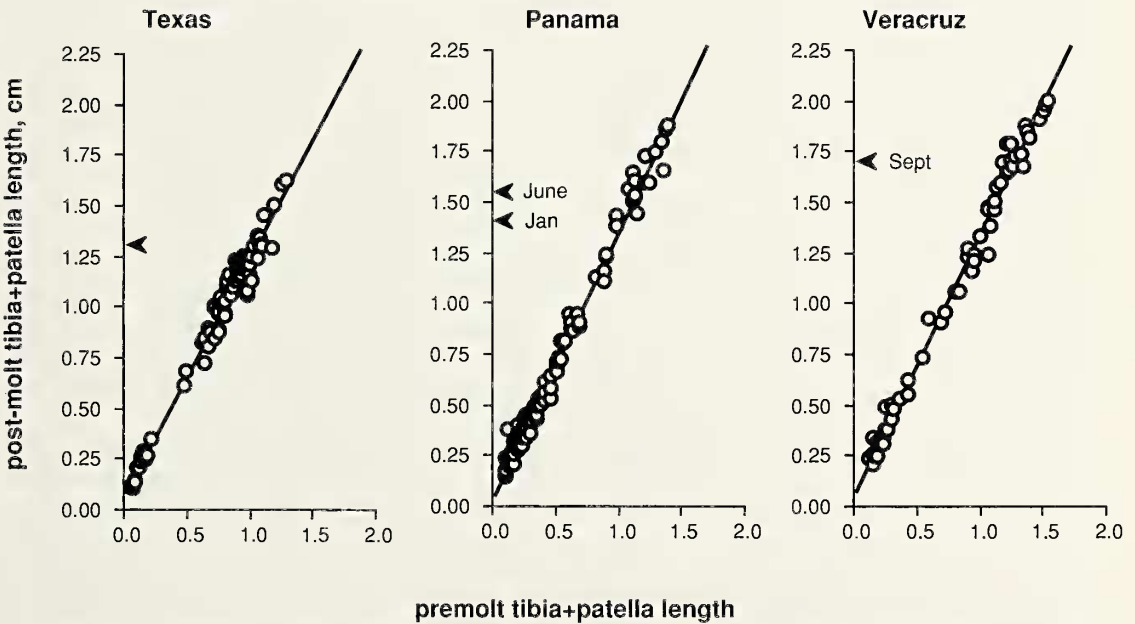


Figure 3.—Pre-molt $t + p$ vs. post-molt $t + p$ for Texas, Panama and Veracruz. The arrows mark the mean adult female size in each population (Y). The two generations in Panama grew at the same rate (dry: $y = 0.047 + 1.300 x$ ($R^2 = 0.970$); wet: $y = 0.050 + 1.310 x$ ($R^2 = 0.985$)). The Veracruz population grew at a similar rate ($y = 0.057 + 1.295 x$ ($R^2 = 0.992$)). The Texas spiders grew significantly less per molt ($y = 0.068 + 1.183 x$ ($R^2 = 0.984$)).

Table 2.—ANCOVA of regression lines of growth per molt: Comparison between the two tropical populations shows no difference in (a) slope or (b) intercept. Comparison of the tropical populations and Texas (c) reveals significant difference in slope.

Source	SS	df	F	P
a. pre-molt size	41.48	1	17 342.9	<0.001
Veracruz vs. Panama (intercept)	0.001	1	0.451	0.503
interaction (effect on slope)	0.000	1	0.193	0.661
error	0.409	171	—	—
b. pre-molt size	42.14	1	17 771.0	<0.001
Veracruz vs. Panama (intercept)	0.001	1	0.28	0.597
error	0.409	172	—	—
c. pre-molt size	43.71	1	6671.25	<0.001
tropical vs. Texas (intercept)	0.007	1	1.06	0.305
interaction (effect on slope)	0.075	1	11.47	0.001
error	1.61	246	—	—

tropical vs. Texas, $n = 250$, $F_{(1, 248)} = 12.30$, $P = 0.001$), suggesting that the Texas spiders hatch at a larger size.

Females matured at different mean sizes in different populations (Fig. 3, Table 3). Comparison of mature female $t + p$ for the two generations on Panama, Veracruz, and Texas indicated that the four groups were significantly different (ANOVA: $F_{(3, 189)} = 70.7$, $P < 0.001$). As the spiders in Panama and Veracruz grew the same amount per molt, the variation in size at maturity within these tropical populations reflects differences in the number of juvenile instars. The small size of females in Texas reflects the lower growth per molt and probably also a lower number of juvenile molts.

Reproduction.—Reproductive effort was measured by the number of eggs and weight of the first egg sac, compared between the two tropical populations as a function of female size ($t + p$), pre-laying weight, and post-laying weight. In addition, some free-living females were observed to lay several egg sacs (uncollected), providing an estimate of the interval between egg sacs. First egg sacs were collected from 15 females on Panama (wet: 9 (June–September); dry: 5 (December–January), 1 (April)). Only two first clutches were collected in Veracruz, but these were included in the analysis for comparison. The low sample size reflects the difficulty of following marked individuals from the last molt to the first oviposition in the dense Veracruz vegetation. There was no significant difference in tibia + patella length or final weight among females sampled between the generations on Panama. Fe-

male size and final pre-laying weight were correlated and there was an effect of site/season (Fig. 4. ANCOVA $t + p$: $F_{(1, 11)} = 10.494$, $P = 0.008$; site/season: $F_{(2, 11)} = 5.296$, $P = 0.024$ (excluding the April female because of undue influence in the regression)). This reflects a relatively higher final weight for female spiders of similar tibia + patella length in Panama (June–September) compared to Veracruz and Panama (December–January).

Only two females laid large numbers of infertile eggs (3% and 5% of 1351 and 1170 total eggs, respectively), one from each generation in Panama. The number of good eggs and clutch weight were significantly correlated with the pre-laying weight of the females (Fig. 5) and positively correlated with female size (regression analysis. number of eggs: slope = 956, $R^2 = 0.30$, $F_{(1, 13)} = 5.50$, $P = 0.035$; clutch weight (g): slope = 0.553, $R^2 = 0.15$, $F_{(1, 13)} = 2.24$, ns). There was no effect of site or season on the relationship between female size and fecundity. Nor were there differences between generations on Panama in clutch weight ($n = 17$, Kruskal-Wallis = 2.44, $df = 2$, ns) or egg number ($n = 17$, Kruskal-Wallis = 1.38, $df = 2$, ns). Relative clutch mass (RCM) was high; females laid on average 104% of their post-laying weight in eggs (range 80–129%) (Table 3). RCM did not vary with female size or with site/season (ANCOVA: no interaction effect. $t + p$: $F_{(1, 14)} = 0.74$, ns; site/season: $F_{(2, 14)} = 1.15$, ns). Non-egg weight gain was estimated by comparing estimated post-molt weight to post-laying weight for five females, four in Panama and one in Veracruz. In these females,

Table 3.—Mean female size (leg I tibia + patella, t + p) at maturity and fecundity data for first egg sacs collected in Panama and Veracruz; mean female size in Texas. RCM: relative clutch mass (=clutch mass/post-laying weight); mean egg weight considers only viable eggs (=weight of good eggs/*n* good eggs). * (ANOVA *P* < 0.001), § (Fisher PSLD *P* < 0.05).

Generation	Mean t + p (SD, <i>n</i>)	Number of egg sacs	Mean post-laying weight (SD)	RCM	Mean egg wt (SD)
Panama June	1.57 (0.14, 83)*	10	0.933 (0.26)	1.08 (0.14)	0.804 (0.06)§
Panama Dec.	1.43 (0.14, 46)*	5	0.809 (0.2)	1.01 (0.15)	0.724 (0.08)§
Veracruz	1.71 (0.15, 38)*	2	1.05	0.93	0.90
Texas	1.31 (0.14, 42)*	0	—	—	—

the weight of the eggs was equal to on average 65% of the weight gained between molting and laying; non-egg weight gain averaged 0.21 g.

The mean egg weight (total weight of good eggs/number of good eggs) was variable (overall range 0.65–0.90 mg) but was not eorrelated with female size, female weight or total number of good eggs (regression analysis. t + p: $F_{(1, 14)} = 0.06$, ns; weight: $F_{(1, 14)} = 1.27$, ns; number of eggs: $F_{(1, 14)} = 0.01$, ns). Within Panama, mean egg weight was greater in June–September clutch-

es than in December–January and April clutches (Table 3; Fisher PSLD = 0.077, *P* < 0.05).

The exact number of days between final molt and first reproduction is known for seven females in Panama and three females in Veracruz. In both populations, females laid within 30 days of the final molt (Panama, range 18–29; Veracruz, range 24–28). Observations of free living females indicate that egg sacs are laid about 20 days apart, and one free-living female in Panama laid five fertile egg sacs.

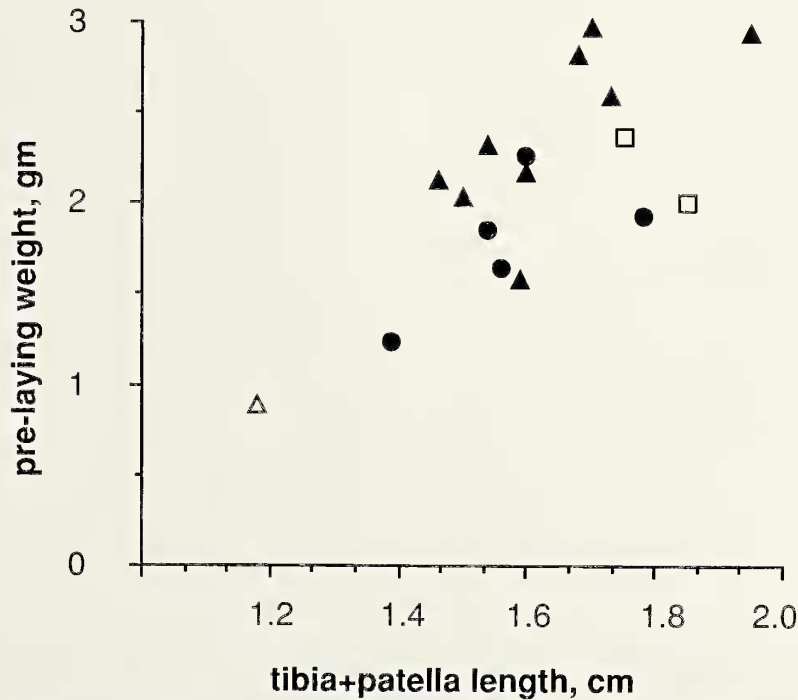


Figure 4.—Estimated adult female pre-laying weight vs. adult size (t + p). The slope is significantly positive, and the June–September females tend to lay at a higher weight for their size. weight = $-1.59 + 2.35(t + p)$, ($R^2 = 0.52$, *n* = 16; April female deleted (see text)). (Δ = Panama April; ▲ = Panama June–September; ● = Panama December–January; □ = Veracruz).

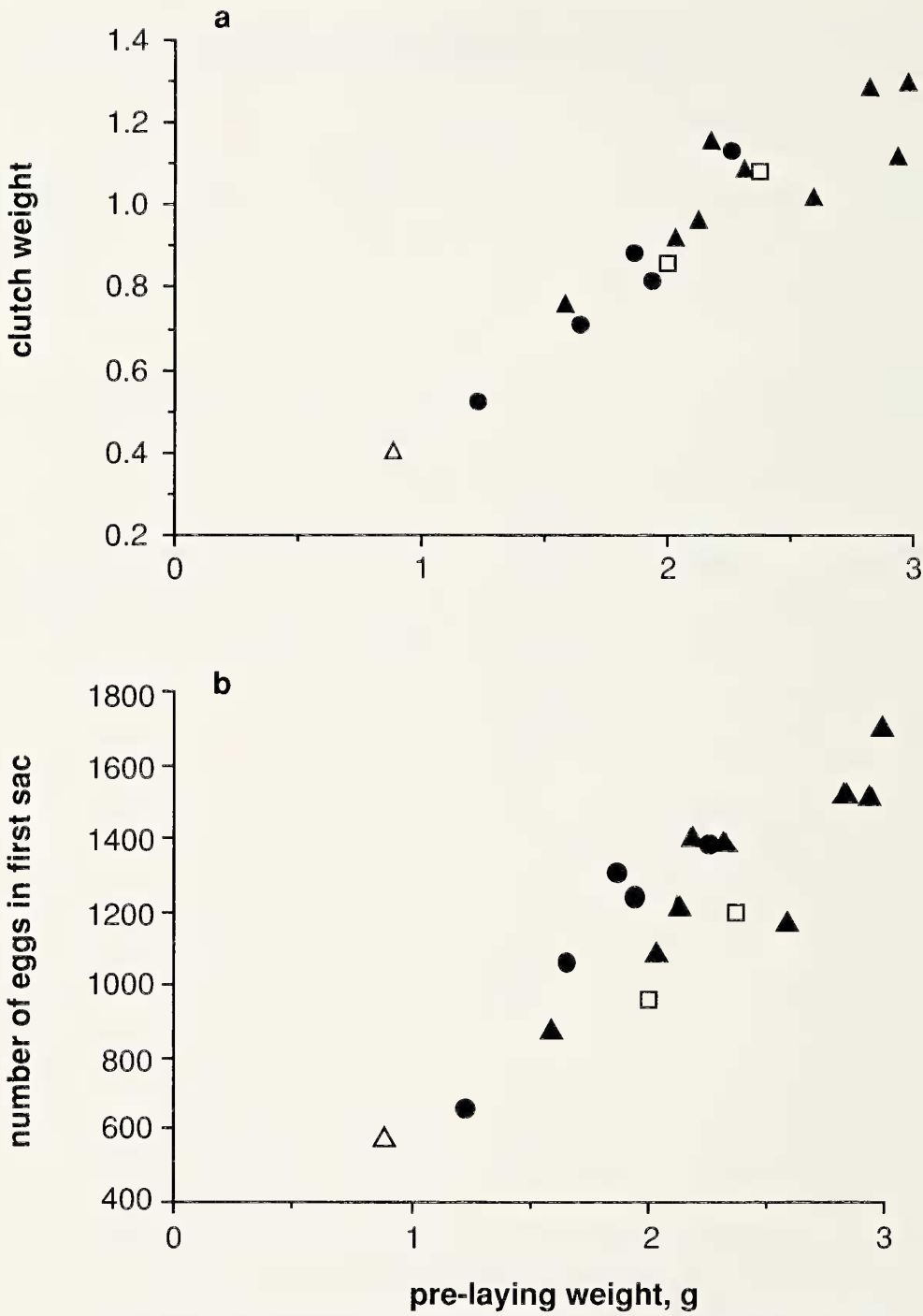


Figure 5.—Female fecundity and clutch weight as a function of estimated pre-laying weight for spiders in the Panama and Veracruz populations. a. Weight of eggs laid: clutch weight = 0.008 + 0.410 (spider weight) ($R^2 = 0.885$). b. The number of eggs laid: $n = 193.4 + 474.7$ (spider weight) ($R^2 = 0.801$). (Δ = Panama April; \blacktriangle = Panama June–September; \bullet = Panama December–January; \square = Veracruz).

DISCUSSION

Nephila clavipes development reflects the interaction of environmentally-induced individual variation and population-specific developmental constraints. Whereas food levels and perhaps also foraging and defensive expenditures can cause changes in growth rates and intermolt intervals, there is little variation within a population in the morphometric relationships involved in molting. This is true for both the size change per molt and in the correlated parameter of pre-molt weight. However, the rate of weight gain, the intermolt interval and the number of juvenile instars vary greatly within and among populations. Variation in female age and size at sexual maturity within populations is probably related to differences in the intermolt interval and number of juvenile instars. The instar at which a female matures appears to reflect individual developmental history and the interaction of the female's chronological age and developmental stage (instar) with the seasonality of the site. Size at sexual maturity and total fecundity are determined by the growth per molt, the number of molts, and the number of egg sacs produced.

Growth per molt in *N. clavipes* is not dependent upon sex or individual foraging success, and minimum growth per molt appears to be population specific. Spiders of the Panama dry-season generation and in Texas have equivalent foraging success, and those of the Panama wet-season generation and in Veracruz have equivalent foraging success (Higgins & Buskirk in press). However, the spiders under dry-season conditions in Panama grew the same amount per molt as those during the Panama wet-season or the Veracruz population. Likewise, in the laboratory experimental differences in prey availability did not affect growth per molt in Panamanian spiders (Higgins pers. obs.). Growth per molt in spiders of both tropical populations was significantly greater than growth per molt by spiders in Texas. The population-specific growth per molt, the lack of variation in size-specific pre-molt weight and the relationship of pre-molt weight to post-molt size imply that the growth per molt is controlled by a population specific minimum pre-molt weight. Increased feeding can cause an individual to "skip" a molt, with a longer intermolt time and greater tibia + patella growth at the molt but reduction of feeding lengthened the intermolt interval without decreasing the growth per molt

(Higgins pers. obs.). The inflexibility of the minimum growth per molt under experimental conditions and between seasons in Panama indicates that the minimum pre-molt weight may have a strong genetic component.

The intermolt interval might therefore be the time required to achieve necessary pre-molt weight. Weight gain is highly plastic and dependent on prey-capture rates (Turnbull 1962; Higgins pers. obs.). An inverse correlation between the rate of weight gain and instar duration in the field was expected from laboratory experiments (Turnbull 1962; Vollrath 1988; Higgins pers. obs.) and failure to observe significant differences in instar duration among populations may have been due to low sample sizes and high within-population variation. The developmental constraint of fixed growth per molt and plastic intermolt interval is distinct from some insects and at least one spider. Larvae of some Lepidoptera and Coleoptera are known to molt even when not gaining weight, apparently constrained by an internal clock mechanism to a maximum intermolt interval (Beck 1950, 1973; Nijhout 1971). Likewise, the spider *Linyphia triangularis* Clerck is reported to molt at a variety of diet-dependent weights (Turnbull 1962). However, the effect of this variation in pre-molt weight on intermolt interval and growth per molt was not presented.

The relative roles of individual history and environment in determining the instar of sexual maturity in spiders is not clear. In other spiders, differences in environmental conditions over small geographic distances are correlated with differences in growth rates (Miyashita 1986), size (instar?) at maturity (Toft 1983; Benton & Uetz 1986), and weight gain by mature females (Wise 1975, 1979; Fritz & Morse 1985). Total development time can be shortened in part through lowered pre-molt weight requirement, corresponding to shorter intermolt periods and resulting in lower growth per molt, manifested as a reduced slope of the developmental trajectory. It is possible that in habitats such as Texas, with low foraging success and strong seasonal changes, the total development time has shortened to permit reproduction before the onset of winter. Mature females in Texas were smallest, reflecting lower growth per molt and probably also maturation at an earlier instar.

Differences among populations in the number of juvenile instars were also related to the length of the growing season. Females in Veracruz, with

the longest growing season (April–August) were largest. Females in Panama alternated, with females of the first generation larger than those of the second generation. The instar of maturity in Panama was inversely related to early juvenile feeding success. The females maturing in June–September were immatures during the season of low foraging success (the dry season), and were larger at sexual maturity than the December–January females. The latter were immatures during the season of high foraging success (the wet season). The inverse relationship with juvenile feeding success is in contrast to earlier laboratory studies, where it was found that male *N. clavipes* matured at an earlier instar under a low, constant feeding regime (Vollrath 1983). The first generation Panama juveniles may be taking advantage of improving environmental conditions (end of the dry season in May) by delaying maturity to a larger instar. Their daughters, juveniles during the rainy season, matured just before or as the dry season began, apparently influenced by the environmental cues heralding the dry season. This hypothesis is supported by their lower pre-laying weight compared to females of the June generation: they oviposited at low weights very early in the dry season before drought conditions were severe. It is striking that neither the relative clutch mass (RCM) nor the number of eggs per clutch were lowered; the lower mean egg weight may be a necessary compensation for maintaining the high number of eggs. The consequences of differences in egg size to offspring size and survivorship are unknown.

Female size and weight gain after sexual maturity are correlated with fecundity in clutch weight and number of eggs (Benton & Uetz 1986; Miyashita 1986; Harrington 1978; Wise 1975; Eberhard 1979; McLay & Hayward 1987). As in *N. clavipes*, most post-molting weight gain by mature female *L. triangularis* was involved in egg production (Turnbull 1962). *N. clavipes* has a high RCM compared to other species of spiders (McLay & Hayward 1986). The size independence of RCM has been found for spiders of six other families (McLay & Hayward 1987), pillbugs (Lawlor 1976) and in several species of snakes (Seigel, Fitch & Ford 1986).

Commitment to sexual maturity in female *N. clavipes* probably reflects a complex interaction between female chronological age, instar, and environmental seasonality. Because an individual in the penultimate instar has partially developed

sexual characters, commitment to sexual maturity is triggered at least two instars before sexual maturity, the ante-penultimate instar. Two instars before maturity at the end of the Panamanian rainy season corresponds to commitment in October and November, preceding the onset of the dry season by at least two months. Several factors occurring in these months might function as cues: changing photoperiod, the steady decline in insect abundance between June and September (Olive 1981; Smythe 1982), and increased rainfall in October and November (D. Winsor, pers. comm.).

In contrast, the arrival of the first winter storm in coastal Veracruz is apparently not heralded by cues to which the spiders respond. This weather shift is temporally highly variable (occurring between September and December), and in 1986 many individuals did not reproduce before they disappeared with the early October onset of the winter storms (Higgins pers. obs.). These individuals were perhaps "taking a chance" in growing larger, increasing their reproductive output through greater potential size, but risking total failure if the weather changed before they could lay (Lawlor 1976) or perhaps were delayed by late emergence or poor foraging conditions.

The phenology of *N. clavipes* in each location reflects a complex interaction between environmental constraints and developmental constraints and plasticity. These spiders have some ability to modulate their development: weight gain and intermolt times are altered by changes in prey availability (Higgins pers. obs.), and the differences in growth per molt between temperate and tropical populations may reflect local adaptation to the differing strength of seasonality (Toft 1983; Baldwin & Dingle 1986). The number of generations per year in populations of *N. clavipes* thus far studied appears to be externally regulated (pers. obs.) and therefore there is probably a greater increase in r (the intrinsic rate of increase) by increasing individual fecundity than by shortening generation time (Stearns & Koella 1986). The relative fitness of individual females, as measured by fecundity, is dependent upon all of these factors as they affect growth, size at maturity, and successful anticipation of seasonal changes in weather.

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